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# Impact of the biocontrol agent *Eccritotarsus catarinensis*, a sap-feeding mirid, on the competitive performance of waterhyacinth, *Eichhornia crassipes*

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## Abstract

The mirid, *Eccritotarsus catarinensis*, was released in South Africa to aid in the biological control of waterhyacinth (*Eichhornia crassipes*). Post-release evaluations are needed to quantify the mirid's impact on the weed in South Africa. The subtle feeding damage that it causes is not easily measured, but studies have shown that interactions with other plant stresses, e.g., plant competition, can often magnify impacts of plant-feeding insects. The impact of the mirid was therefore evaluated using an additive series analysis of competition between waterhyacinth and waterlettuce (*Pistia stratiotes*), as influenced by mirid herbivory. Competitive abilities of waterlettuce and waterhyacinth were determined using an inverse linear model with plant weight as the yield variable. In the absence of herbivory, waterhyacinth was 23 times more competitive than waterlettuce, but only 10 times more competitive when exposed to mirid feeding. Waterlettuce was only 0.9 times as aggressive as waterhyacinth that was free of herbivory, but 1.5 times as competitive when mirids were impacting waterhyacinth. Most importantly, in the presence of herbivory on waterhyacinth, interspecific competition coefficients from waterhyacinth on waterlettuce were no longer statistically significant. These results show that the mirid destabilizes waterhyacinth's competitive interactions between these two floating plant species, although impacts were subtle. This insect is unlikely to be an effective agent by itself, but it will be a useful complement to the existing biological control agents in South Africa.
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## 1. Introduction

Waterhyacinth (*Eichhornia crassipes* (Mart.) Solms-Laub (Pontederiaceae)) has achieved international notoriety as the world's worst aquatic weed (Holm et al., 1977), and has, as a result, been targeted for biological control in several countries (Harley, 1990). At least seven natural enemies have been used for this purpose

worldwide (Julien and Griffiths, 1998). Some have successfully controlled waterhyacinth in tropical regions, such as Papua New Guinea (Julien and Orapa, 1999) and Lake Victoria in Uganda (Cock et al., 2000). However, additional agents are being considered for release in more temperate regions, such as South Africa and North America, where results have been more variable (Cordo, 1999; Stanley and Julien, 1999).

Five arthropod natural enemies of waterhyacinth have been released in South Africa, and more are being considered (Hill and Cilliers, 1999). The mirid *Eccrito-*

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*tarsus catarinensis* (Carvalho) (Heteroptera: Miridae) was introduced in 1996 (Hill et al., 1999) and, although populations have established, its performance has yet to be assessed. Inasmuch as each new biocontrol agent might present additional risk to the native flora (Simberloff and Stiling, 1996), assessments of the performance of existing agents are needed to determine whether further introductions are warranted.

Even though it is fundamentally important to understand the effects of biological control agents on native flora, typically, their effectiveness is almost always assessed by measuring their direct effects on the target weeds (Callaway et al., 1999). However, impacts are often sublethal and experiments fail to detect subtle effects that accrue over time and provide significant long-term control. Furthermore, feeding damage by sap-feeding insects is often inconspicuous and without overt symptoms. Attention has therefore recently focused on exploiting the interaction between herbivory and plant competition, and their combined effects on plant performance, as a means of assessing the value of new agents (e.g., Ang et al., 1994; Story et al., 2000; Van et al., 1998).

The effects of biological control agents that do not inflict direct mortality on the target plant can be difficult to measure. It has been suggested that the impact of invertebrate herbivory will become more noticeable when grazed plants are competing with other plants for resources, due to a gradual reduction of the host plant's vigor (Center et al., 2001). Therefore, any reduction in the competitive ability of grazed plants may be sufficient to increase their susceptibility to competition from other plants (Cottam, 1986; Whittaker, 1979). Thus, a fundamental justification for using biological control agents to suppress invasive plants is that by weakening the invader, indigenous species may gain a competitive advantage (Callaway et al., 1999). Furthermore, Crawley (1989) noted that the principal effect of herbivores is not caused by them eating the plants to extinction, but more often from their feeding modifying the relative competitive abilities of the plants with one another.

Biological control studies conducted to determine the combined effect of herbivory and plant competition on plant performance have shown that by combining strong plant competitors with biological control agents, the control obtained exceeds that exerted by either mechanism alone (e.g., Ang et al., 1994; Story et al., 2000; Van et al., 1998). When grown together in the absence of natural enemies, waterhyacinth dominates waterlettuce in nutrient enriched waters (Agami and Reddy, 1990). Therefore, if this interaction changes in the presence of herbivory, we can assume that the biological control agent has reduced the vigor, and therefore the competitive ability, of waterhyacinth.

*Eccritotarsus catarinensis*, a sap-sucking mirid, produces damage that is not usually lethal to the plant (Hill et al., 1999). Because no biocontrol agent comes without risks, and because of doubts as to potential benefits of the mirid, we employed competition studies to magnify, and thereby quantify, subtle sublethal effects of its feeding. The mirid does not feed on waterlettuce (Hill et al., 1999), another floating species that commonly coexists with waterhyacinth, so it was chosen as the competing species.

This study follows the protocol employed by Pantone et al. (1989), who suggested competition experiments using an additive series, and the application of the inverse linear model as effective methods for evaluating the efficacy of potential control agents. These methods provide biologically meaningful competition coefficients, which will allow for direct comparison with other similar competition studies.

## 2. Materials and methods

Waterhyacinth and waterlettuce were grown outdoors in plastic tubs at the University of the Witwatersrand, Johannesburg, to determine competitive interactions between the two plant species. Both plants were obtained from stock cultures maintained at the university. The experimental design employed an additive series (Spitters, 1983) of factorial combinations of different densities of the two species in a randomized block design. The waterhyacinth:waterlettuce densities were 0:3, 0:9, 3:0, 3:3, 3:9, 9:0, 9:3, and 9:9 plants per container. The waterhyacinth:waterlettuce density matrices were repeated twice—one series as a control without insects and the other with the mirid *E. catarinensis* in a randomized block design. The two matrices were repeated three times, resulting in 48 tubs of different plant combinations.

The plastic tubs (51 cm by 40 cm and 28 cm deep) were filled with 23 L water. Nitrogen and phosphorus were added as potassium nitrate ($KNO_3$) and potassium dihydrogen orthophosphate ($KH_2PO_4$), respectively, at concentrations of 50.5 mg N/L and 2.56 mg P/L, the concentrations at which maximum N storage occurs in waterhyacinth (Reddy et al., 1989, 1990). A commercial iron chelate (13% Fe) was also added to the water at a concentration of 2 g/23 L of water. Water and nutrients were replaced weekly. Each plastic tub was enclosed by a net canopy.

Two weeks later, all daughter ramets were removed from the plants to reestablish the prescribed stocking densities. Thereafter, 15 insects per waterhyacinth plant, collected randomly from the Plant Protection Research Institute in Pretoria, South Africa, were released into each cage. The male:female ratio was not controlled as the mirid exhibits a 50:50 sex ratio. Feeding damage to the waterhyacinth plants and mirid numbers were monitored visually for the first 4 weeks to ensure that the

mirids had established and were feeding on waterhyacinth. It was not viable to monitor insect density during the course of the experiment because the disturbance would have been too disruptive to the plants and the insects.

After 16 weeks, the insects were removed, the number of adults was counted, the presence of nymphs was noted, and the plants were harvested. In each tub, the two plant species were separated and the total biomass (fresh weight), including daughter plants, of each species was measured. These wet weight values were then divided by the original plant stocking density to obtain mean wet-weight. Dead plant material was not removed prior to weighing. Fresh weight was measured instead of dry weight because both measures are highly correlated (T.D. Center, unpublished data), and fresh weight was the more expedient measure.

Data were analyzed using the inverse linear model as described by Spitters (1983) and Pantone et al. (1989). This model involves multiple linear regressions of the inverse of the mean weight-yield of each species as the dependent variable, on the planting densities of waterhyacinth and waterlettuce, used as the independent variables. The regression equation is of the form:

$$1/w_h = a_{h0} + a_{hh}d_h + a_{hl}d_l,$$

$$1/w_l = a_{l0} + a_{ll}d_l + a_{lh}d_h.$$

Here $1/w_h$ and $1/w_l$ are the inverse biomass yields of individual waterhyacinth and waterlettuce plants, respectively, and $d_h$ and $d_l$ represent their respective planting densities. The coefficients $a_{hh}$ and $a_{ll}$ estimate intraspecific competition, while the coefficients $a_{hl}$ and $a_{lh}$ estimate interspecific competition, in terms of their effects on reciprocal waterhyacinth or waterlettuce yield. The intercepts ($a_{h0}$ and $a_{l0}$) measure the reciprocal of the maximum weight of isolated plants. The ratios of the coefficients $a_{hh}/a_{hl}$ and $a_{ll}/a_{lh}$ measure the effects of intraspecific competition by waterhyacinth and waterlettuce, respectively, on their own yield relative to the effects of interspecific competition by one species on the yield of the other (Pantone et al., 1989).

The regressions were weighted using biomass as the weighting variable because the wet weight ($w_h$ and $w_l$) variance decreased as plant biomass increased. Therefore, greater wet weights values influenced the regression more than smaller ones (Spitters, 1983). Regressions for the control series and insect-treated series were compared using multiple regression analysis (Zar, 1996). An indicator variable was used to distinguish between the presence and absence of the control agent, and $F$ tests of regressions of the pooled data determined whether the competition coefficients were significantly different as a result of herbivory by the mirid.

For each experimental unit, the mean end-weights per original plant (i.e., total yield/planting density) were cal-culated for both waterhyacinth and waterlettuce, in the presence or absence of herbivory on waterhyacinth. Mann–Whitney $U$ tests were used to analyze whether the mean end-weights of waterhyacinth and waterlettuce, were significantly different in the presence and absence of mirid herbivory.

## 3. Results

After 4 weeks, a visual assessment of each tub in which mirids had been released confirmed the presence of feeding damage to the waterhyacinth leaves. At the end of 16 weeks, the mean number of adult mirids collected per plant, for the original planting densities, was $37.25 \pm 10.96$, and nymphs were present in every tub in which adults had been released, indicating that the mirid populations were well established.

### 3.1. Waterhyacinth

Waterhyacinth remained the dominant species after 16 weeks of selective feeding by the mirid, but its competitive advantage over waterlettuce decreased as reflected by the ratios of respective competition coefficients ($a_{hh}/a_{hl}$). Waterhyacinth without herbivory was at least 23 times ($P < 0.05$) more competitive than waterlettuce, but only 10-fold greater with sustained damage from mirid feeding ($P < 0.05$), indicating a 56% decrease in competitive ability (Table 1). Tests of the pooled data indicate that the main effects of the regression equations were significantly different due to herbivory ($F_{1, 32} = 7.76$, $P = 0.009$).

These data were also graphically analyzed as three-dimensional, surface–response planes where the slope in one direction represents the effect of waterhyacinth's own density upon its yield, and the slope in the other direction represents the effects of waterlettuce density on waterhyacinth yield (Fig. 1). The flat slope of the waterlettuce density regression planes in both the herbivory treatment and the control indicated that interspecific competition from waterlettuce was negligible. Waterlettuce had little effect on waterhyacinth yield either with (waterlettuce density $\beta = -0.05$) or without herbivory (waterlettuce density $\beta = -0.17$). However, the steep slope of the waterhyacinth regression planes showed that intraspecific competition significantly affected waterhyacinth yield with (waterhyacinth density $\beta = 0.917$) or without (waterhyacinth density $\beta = 0.870$) herbivory.

### 3.2. Waterlettuce

Waterlettuce was obviously the weaker competitor inasmuch as adding one waterlettuce plant ($a_{ll}/a_{lh} = 0.974$, $P < 0.005$) had the same impact on waterlettuce

Table 1
Multiple regression analysis of the effects of *Eccritotarsus catarinensis* herbivory and plant density on the reciprocal of waterhyacinth yield[a] and waterlettuce yield [b] (wet weight (g))

| Treatment | Regression coefficients | | | Intercept | $R^2$ | F value (P) |
|---|---|---|---|---|---|---|
| Waterhyacinth | $a_{hh}$ | $a_{hl}$ | $a_{hh}/a_{hl}$ | $a_{h0}$ | | |
| E. catarinensis absent | 0.243 | −0.010 | 23.631 | 0.5214 | 0.755 | 23.11 (<0.05) |
| E. catarinensis present | 0.182 | −0.0181 | 10.007 | 0.6086 | 0.856 | 44.61 (<0.05) |
| Waterlettuce | $a_{ll}$ | $a_{lh}$ | $a_{ll}/a_{lh}$ | $a_{l0}$ | | |
| E. catarinensis absent | 8.650 | 8.886 | 0.974 | −46.853 | 0.690 | 16.67 (<0.05) |
| E. catarinensis present | 3.294 | 2.069 | 1.592 | −6.392 | 0.460 | 6.40 (<0.05) |

[a] The intercepts $a_{h0}$ estimate the reciprocal of the maximum weight of isolated waterhyacinth plants. The regression coefficients $a_{hh}$ and $a_{hl}$ measure intraspecific and interspecific competition respectively, for waterhyacinth. The ratio $a_{hh}/a_{hl}$ measures the effects of intraspecific competition by waterhyacinth on its own weight relative to the effects of interspecific competition by waterlettuce.

[b] The intercepts $a_{l0}$ estimate the reciprocal of the maximum weight of isolated waterlettuce plants. The regression coefficients $a_{ll}$ and $a_{lh}$ measure intraspecific and interspecific competition, respectively, for waterlettuce. The ratio $a_{ll}/a_{lh}$ measures the effects of intraspecific competition by waterlettuce on its own weight relative to the effects of interspecific competition by waterhyacinth.
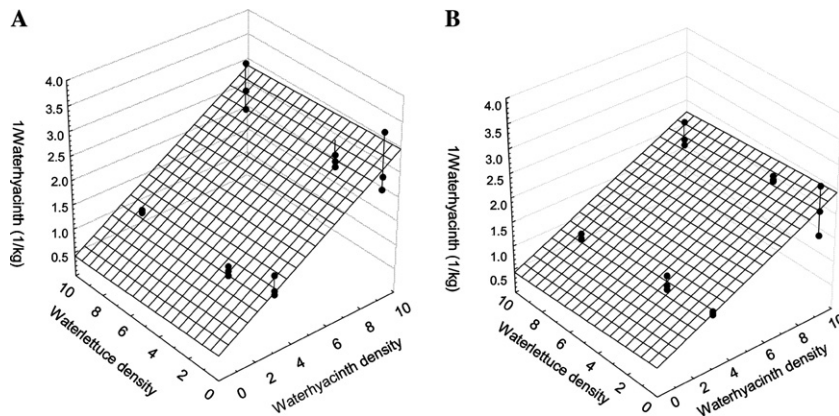


Fig. 1. Multiple regression planes indicating the combined effects of waterlettuce and waterhyacinth densities on the reciprocal of the mean wet weight (1/kg) per waterhyacinth plant (i.e., higher values represent lower yield). (A and B) Compare relative competitive abilities of waterhyacinth in the absence and presence of *E. catarinensis* feeding damage, respectively. Points indicate observations ($n = 18$) and the vertical lines between data points represent the residuals. Values on $X$ and $Y$ axes represent waterlettuce and waterhyacinth planting densities at the outset of the experiment.

yield as adding one waterhyacinth plant without herbivory, but in the presence of the mirid, this ratio increased to 1.6 ($P < 0.05$) (Table 1). Tests of the pooled data indicated that the main effects of the regression equations were significantly different due to herbivory ($F_{1, 32} = 6.50$, $P = 0.016$).

The three-dimensional surface response planes were again used to determine the effects of intra- and interspecific competition on waterlettuce yield (Fig. 2). In the insect-free control, both waterhyacinth and waterlettuce planting densities significantly affected the wet weight of waterlettuce, indicated by the steep gradients in both directions (waterhyacinth density $\beta = 0.568$, waterlettuce density $\beta = 0.436$) (Fig. 2A). Therefore, both inter- and intraspecific competition were operative when there was no influence of herbivory. However, this relationship changed in the presence of mirids and only intraspecific competition significantly affected waterlettuce yield (waterhyacinth density $\beta = -0.21$; waterlettuce density $\beta = 0.625$) (Fig. 2B), indicating that its compet-

itive ability had increased; while waterhyacinth's competitive ability had decreased.

There was no significant difference between the mean end-weights per original waterhyacinth plant, in either the insect-free control or the herbivory treatment (original planting density of three waterhyacinth plants: $U_{9;9} = 32.5$, $P > 0.05$; original planting density of nine waterhyacinth plants: $U_{9;9} = 18.5$, $P > 0.05$) (Fig. 2A). Similarly, there was no significant difference between the mean end-weights per original waterlettuce plant for either treatment (original planting density of three waterlettuce plants: $U_{9;9} = 33.5$, $P > 0.05$; original planting density of nine waterlettuce plants: $U_{9;9} = 39.0$, $P > 0.05$) (Fig. 2B).

## 4. Discussion

Previous studies have demonstrated the superior competitive nature of waterhyacinth when grown in cul-
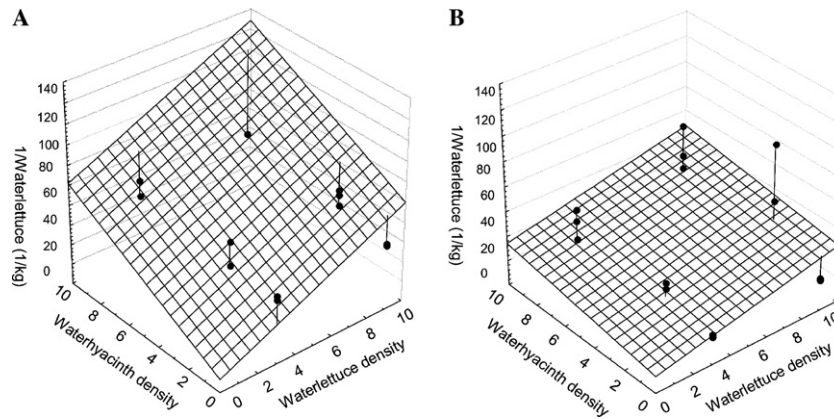
Fig. 2. Multiple regression planes indicating the combined effects of waterhyacinth and waterlettuce densities on the reciprocal of the mean wet weight (1/kg) per waterlettuce plant. (A and B) Compare relative competitive abilities of waterlettuce in the absence and presence of *E. catarinensis* feeding damage to waterhyacinth, respectively. Points indicate observations ($n = 18$) and the vertical lines between data points represent the residuals. Values on *X* and *Y* axes represent waterhyacinth and waterlettuce planting densities at the outset of the experiment.

ture with waterlettuce (Agami and Reddy, 1990; Sutton, 1983; Tag El Seed, 1978). Waterhyacinth shades and stresses waterlettuce plants through its high productivity and morphological plasticity (Agami and Reddy, 1990). However, in this study, herbivory by *E. catarinensis* reduced the vigor of waterhyacinth growing in culture with waterlettuce and correspondingly increased the relative competitive ability of waterlettuce. Therefore, the most significant finding of our study is that mirid herbivory reduced waterhyacinth's competitive ability in two ways. First, the effects of interspecific competition from waterhyacinth on waterlettuce yield became negligible when the mirid was present, as indicated by the flat regression plane (Fig. 2); and second, there was a 56% reduction in intraspecific competition by waterhyacinth (Table 1).

We had expected waterhyacinth wet weight to be significantly less, and waterlettuce wet weight to be greater, in the presence of herbivory, but no difference was evident. Compensation for herbivory might explain why there was no reduction in waterhyacinth yield. Generally, plant–herbivore interactions are considered antagonistic because of the negative direct effects herbivores have on plants, through biomass consumption (De Mazancourt and Loreau, 2000). However, the grazing optimization hypothesis has challenged this theory by suggesting that herbivores can enhance plant primary production under certain conditions, where low grazing intensity will increase primary production up to an optimum at medium grazing intensity, after which production will decrease as grazing increases (Dyer et al., 1986; Hilbert et al., 1981). The initial insect inoculation was small and the extent of feeding damage observed in this experiment was not extreme, and might be classified as low to intermediate intensity, which could explain why waterhyacinth production was not affected by herbivory. Other experiments that

employed the same nutrient levels in the growth media have shown that under high mirid feeding intensity, the number of waterhyacinth leaves, and shoot offsets is reduced (Coetzee, 2003). Furthermore, compensation for herbivory by waterhyacinth may have been a short-term phenomenon. Had the study been allowed to continue longer so that the mirid population could increase, reduction in waterhyacinth yield might have been more evident. However, if we had allowed the experiment to go on for much longer, we might have missed seeing the effect of competition. Therefore, determining the proper length of time for these experiments is difficult.

In addition, compensation might have been possible because of the high nitrogen (N) concentration in the nutrient media. Sap feeders, such as the mirid, remove N from the plant, but waterhyacinth exhibits high consumption of N in high nutrient conditions (Gossett and Norris, 1971; Reddy et al., 1989, 1990), so there may have been N to spare for the mirid to consume. Under low nutrient conditions, we expect the effects of mirid herbivory on waterhyacinth yield to be more severe.

The concentrations of N and P used in this study are very high, but are realistic values in that they are the threshold concentrations for N storage of waterhyacinth (Reddy et al., 1989, 1990). According to South African Water Quality standards, the N and P concentrations used are hypertrophic (Walmsley, 2000), and impoundments exist in South Africa with N and P concentrations similar to those used in this study (e.g., Naicker et al., 2003). A study conducted at Hammarsdale Dam (KwaZulu Natal Province, South Africa) concluded that a site close to a wastewater inlet was hypertrophic (1.561 mg/N/L and 0.731 mg/P/L) (Oberholzer, 2002). Both *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae), another waterhyacinth control agent, established at this site since 1989, and *E. catarinensis*,

established here since 1996, have reached very high population densities but appear to have had little impact on the waterhyacinth infestation (Hill and Olckers, 2000). It is predicted that the hypertrophic conditions have negated the effects of herbivory by these two control agents. Thus, efficacy of an agent is difficult, if not impossible, to predict prior to its release. Perhaps the mirid will be more effective when nutrients are less available to the plant.

Using competition experiments such as this to evaluate the efficacy of a new control agent of waterhyacinth has many advantages. Individuals of both competing species are easily identifiable. Also, the nutrient status of the water is easily controlled, and the critical criterion, wet weight, is easily measured. Because the effect of feeding damage by *E. catarinensis* on waterhyacinth vigor is subtle, it is difficult to measure the direct effects of the mirid. Waterhyacinth has a very plastic phenotype in leaf and petiole shape and size, which can be influenced by many factors. Comparative experiments with other biocontrol agents of waterhyacinth, *Neochetina eichhorniae* and *N. bruchi* Hustache (Coleoptera: Curculionidae), have shown that without herbivory, 41 waterlettuce plants produce a competitive effect equivalent to one waterhyacinth plant, while weevil feeding damage reduced this ratio to 0.7 for *N. bruchi* alone, 1.4 for *N. eichhorniae* alone, and 0.6 for the two species together (T.D. Center, unpublished data). By this yardstick, the weevils are more effective control agents, but nonetheless, *E. catarinensis* does reduce waterhyacinth vigor and it should be a valuable adjunct to the existing biological control program.

These data indicate that even though the competitive ability of waterhyacinth is reduced by mirid herbivory, the mirid will not be very effective in high nutrient situations, although competitors might better be able to withstand encroachment by waterhyacinth. In biological control programs, it would be desirable to evaluate the efficacy of a potential control agent prior to its release. Experiments such as those reported here could evaluate the potential value of the new control agent in quarantine, thereby preventing the introduction of questionable agents that might provide little control. While the method has shortcomings (see Center et al., 2001), it is worth considering.

## Acknowledgments

## References

Agami, M., Reddy, K.R., 1990. Competition for space between *Eichhornia crassipes* (Mart.) Solms and *Pistia stratiotes* L. cultured in nutrient-enriched water. Aquat. Bot. 38, 195–208.

Ang, B.N., Kok, L.T., Holtzman, G.I., Wolf, D.D., 1994. Competitive growth of Canada thistle, tall fescue and crownvetch in the presence of a thistle defoliator, *Cassida rubignosa* Müller (Coleoptera: Chrysomelidae). Biol. Control 4, 277–284.

Callaway, R.M., DeLuca, T.H., Belliveau, W.M., 1999. Biological control herbivores may increase competitive ability of the noxious weed *Centaurea maculosa*. Ecology 80, 1196–1201.

Center, T.D., Van, T.K., Hill, M.P., 2001. Can competition experiments be used to evaluate the potential efficacy of new waterhyacinth biological control agents? In: Julien, M.H., Hill, M.P. Center T.D., Jianqing, D. (Eds.), Biological and Integrated Control of Waterhyacinth, *Eichhornia crassipes*. Proceedings of the 2nd Meeting of the Global Working Group for the Biological and Integrated Control of Waterhyacinth, Beijing, China, 9–12 October 2000. ACIAR Proceedings No. 102, pp. 77–81.

Cock, M., Day, R., Herren, H., Hill, M.P., Julien, M.H., Neuenschwander, P., Ogwang, J., 2000. Harvesters get that sinking feeling. Biocontrol News Inf. 21, 1–8.

Coetzee, J.A., 2003. Suitability of *Eccritotarsus catarinensis* as a Biological Control Agent of Water Hyacinth. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

Cordo, H.A., 1999. New agents for biological control of waterhyacinth. In: Hill, M.P., Julien, M.H., Center, T.D. (Eds.), Proceedings of the First IOBC Global Working Group Meeting for the Biological and Integrated Control of Waterhyacinth, 16–19 November 1998, Zimbabwe. Plant protection Research Institute, Pretoria, South Africa, pp. 68–74.

Cottam, D.A., 1986. The effects of slug-grazing on *Trifolium repens* and *Dactylis glomerata* in monoculture and mixed sward. Oikos 47, 275–279.

Crawley, M.J., 1989. Insect herbivores and plant population dynamics. Annu. Rev. Entomol. 34, 531–564.

De Mazancourt, C., Loreau, M., 2000. Grazing optimization, nutrient cycling, and spatial heterogeneity of plant–herbivore interactions: should a palatable plant evolve? Evolution 54, 81–92.

Dyer, M.I., De Angelis, D.L., Post, W.M., 1986. A model of herbivore feedback on plant productivity. Math. Biosci. 79, 171–184.

Gossett, D.R., Norris Jr., W.E., 1971. Relationship between nutrient availability and content of nitrogen and phosphorous in tissues of the aquatic macrophyte, *Eichhornia crassipes* (Mart.) Solms. Hydrobiologia 38, 15–28.

Harley, K.L.S., 1990. The role of biological control in the management of waterhyacinth, *Eichhornia crassipes*. Biocontrol News Inf. 11, 11–22.

Hilbert, D.W., Swift, D.M., Detling, J.K., Dyer, M.I., 1981. Relative growth rates and the grazing optimization hypothesis. Oecologia 51, 14–18.

Hill, M.P., Cilliers, C.J., Neser, S., 1999. Life history and laboratory host range of *Eccritotarsus catarinensis* (Carvalho) (Heteroptera: Miridae), a new potential natural enemy released on waterhyacinth (*Eichhornia crassipes* (Mart.) Solms-Laub.) (Pontederiaceae) in South Africa. Biol. Control 14, 127–133.

Hill, M.P., Cilliers, C.J., 1999. A review of the arthropod natural enemies, and factors that influence their efficacy, in the biological control of waterhyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach (Pontederiaceae), in South Africa. In: Olckers, T., Hill, M.P. (Eds.), Biological Control of Weeds in South Africa (1990–1998). Afr. Entomol. Mem. No. 1, pp. 103–112.

Hill, M.P., Olckers, T., 2000. Biological control initiatives against water hyacinth in South Africa: constraining factors, success and new courses of action. In: Julien, M.H., Center, T.D., Hill, M.P.

(Eds.), Proceedings of the Second Global Working Group Meeting for the Biological and Integrated Control Water Hyacinth. Beijing, China, 9–12 October 2000.

Holm, L.G., Plucknett, D.L., Pancho, J.V., Herberger, J.P., 1977. The World's Worst Weeds. Distribution and Biology. University Press of Hawaii, Honolulu, Hawaii.

Julien, M.H., Orapa, W., 1999. Structure and management of a successful biological control project for waterhyacinth. In: Hill, M.P., Julien, M.H., Center, T.D. (Eds.), Proceedings of the First IOBC Global Working Group Meeting for the Biological and Integrated Control of Waterhyacinth, 16–19 November 1998, Zimbabwe. Plant protection Research Institute, Pretoria, South Africa, pp. 123–134.

Julien, M.H., Griffiths, M.W., 1998. Biological Control of Weeds: A World Catalogue of Agents and their Target Weeds, fourth ed. C.A.B.I. Publishing, CAB International, Oxon, UK.

Naicker, K., Cukrowska, E., McCarthy, T.S., 2003. Acid mine drainage arising from gold mining activity in Johannesburg, South Africa and environs. Environ. Pollut. 122, 29–40.

Oberholzer, I.G., 2002. The Effect of Nutrient Rich Water on Biological Control of Water Hyacinth. M.Sc. Thesis, University of Pretoria, Pretoria, South Africa.

Pantone, D.J., William, W.A., Maggenti, A.R., 1989. An alternative approach for evaluating the efficacy of potential biocontrol agents of weeds. 1. Inverse linear model. Weed Sci. 37, 771–777.

Reddy, K.R., Agami, M., Tucker, J.C., 1989. Influence of nitrogen supply rates on growth and nutrient storage by water hyacinth (Eichhornia crassipes) plants. Aquat. Bot. 36, 33–43.

Reddy, K.R., Agami, M., Tucker, J.C., 1990. Influence of phosphorus supply on growth and nutrient storage by water hyacinth (Eichhornia crassipes) plants. Aquat. Bot. 37, 355–365.

Simberloff, D., Stiling, P., 1996. How risky is biological control? Ecology 77, 1965–1974.

Spitters, C.J.T., 1983. An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. Neth. J. Agric. Sci. 31, 1–11.

Stanley, J.N., Julien, M.H., 1999. The host range of Eccritotarsus catarinensis (Heteroptera: Miridae), a potential agent for the biological control of water hyacinth (Eichhornia crassipes). Biol. Control 14, 134–140.

Story, J.M., Good, W.R., White, L.J., Smith, L., 2000. Effects of the interaction of the biocontrol agent Agapeta zoegana L. (Lepidoptera: Cochylidae) and grass competition on spotted knapweed. Biol. Control 17, 182–190.

Sutton, D.L., 1983. Aquatic plant competition. Aquatics 5, 10–14.

Tag El Seed, M., 1978. Effect of pH on the nature of competition between Eichhornia crassipes and Pistia stratiotes. J. Aquat. Plant Manag. 16, 53–57.

Van, T.K., Wheeler, G.S., Center, T.D., 1998. Competitive interactions between hydrilla (Hydrilla verticillata) and vallisneria (Vallisneria americana) as influenced by insect herbivory. Biol. Control 11, 185–192.

Walmsley, R.D., 2000. Perspectives on eutrophication of surface waters: Policy/research needs in South Africa. WRC Report KV129/00. Water Research Commission, Pretoria, South Africa.

Whittaker, J.B., 1979. Invertebrate grazing, competition and plant dynamics. In: Anderson, R.M., Turner, B.D., Taylor, L.R. (Eds.), Population Dynamics. The 20th Symposium of the British Ecological Society, London, 1978. Blackwell Scientific Publications, Oxford.

Zar, J.H., 1996. Biostatistical Analysis, third ed. Prentice Hall, London.